

Application of Catch-Survey Models to the Northern Shrimp Fishery in the Gulf of Maine

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Abstract.—The fishery for northern shrimp *Pandalus borealis* in the Gulf of Maine was modeled to assess the impacts of recent increases in fishing effort and landings. A Collie–Sissenwine analysis of landings and research vessel survey data from 1985 to 1997 indicates that instantaneous annual fishing mortality rate (F) substantially increased in the last 2 years and reduced the stock to a low level of abundance. A nonequilibrium surplus production model (ASPIC) of 1968–1997 landings and survey indices provides similar results. Estimates of F ranged from 0.1 to 0.5 for 1985–1995 and increased to 0.7 in 1996 and to 0.9 in 1997, while abundance of northern shrimp decreased in 1998 to the lowest level since the early 1980s. Fishing mortality rates greater than 0.6 were associated with a stock collapse in the 1970s, suggesting that stock biomass decreased when spawning potential was reduced to less than 10% of maximum. In the absence of reliable stock–recruitment information, $F_{20\%}$ (0.63) may be a precautionary overfishing threshold. Based on a decade of relatively stable stock levels, an appropriate management target may be an F of 0.34, the average value from 1985 to 1995. At $F = 0.34$, egg production per recruit is 40% of maximum. The present methods provide a more objective basis for fishery management decisions than the qualitative methods that were previously applied to this stock and may perform well for other fish stocks that lack accurate information on age structure.

Northern shrimp *Pandalus borealis* are distributed discontinuously throughout boreal waters of the northern hemisphere (Shumway et al. 1985). Northern shrimp in the Gulf of Maine are considered to constitute a unit stock at the southern extent of the species' Atlantic range (Haynes and Wigley 1969) where they inhabit cold waters and soft mud bottom off New England (Schick 1991). Low temperatures appear to positively influence abundance of the Gulf of Maine stock (Dow 1977; Apollonio et al. 1984). Northern shrimp are protandrous hermaphrodites. In the Gulf of Maine, they generally spawn as males in their third year then begin to transform into mature females and spawn in their fourth year. Oviparous females move into coastal

waters in early winter. Eggs hatch inshore, and juveniles migrate to deeper offshore waters as they begin to mature (Shumway et al. 1985).

A directed otter trawl fishery for northern shrimp began in coastal waters of Maine and Massachusetts during winter months in the 1930s (Scattergood 1952). The fishery expanded rapidly during the 1960s to offshore areas, with fishing occurring throughout the year by vessels from Maine, New Hampshire, and Massachusetts. Landings peaked from 1969 to 1972, which was followed by a stock collapse in the late 1970s (Clark 1981, 1982; Clark and Anthony 1981). The fishery was closed by regulation in 1978. Under restricted fishing seasons and gear regulations (minimum mesh size and eventually finfish exclusion devices), the resource grew to support a relatively stable and valuable fishery (1996 landed value was US\$15 million; NMFS 1997). The fishing season

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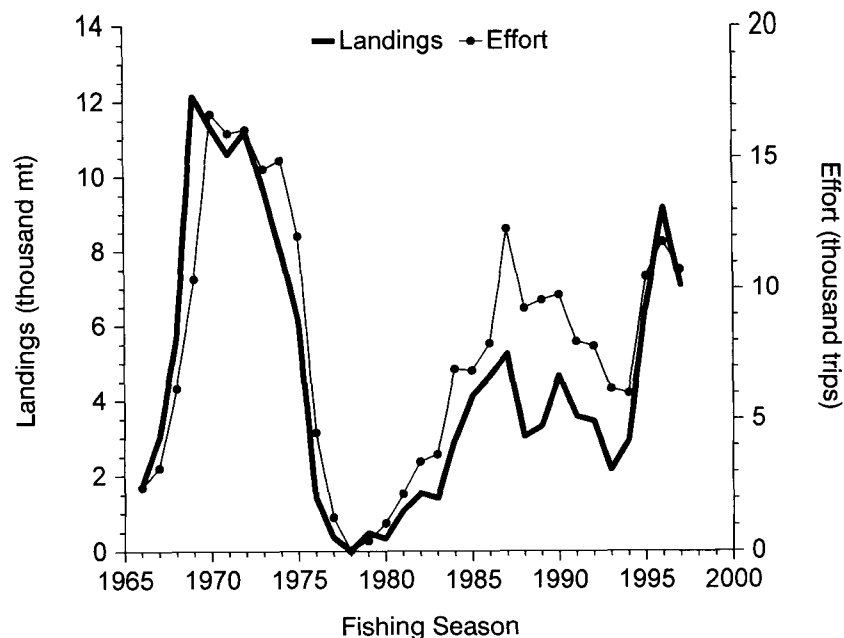


FIGURE 1.—Gulf of Maine northern shrimp landings and nominal effort. All fishing trips used a shrimp otter trawl; mt is metric tons.

is currently limited to December through May, with the majority of northern shrimp landed in January and February. Northern shrimp are landed exclusively in coastal states of the Gulf of Maine. Fishing effort has substantially increased in recent years (Figure 1), partly as a result of displaced effort from the restricted New England groundfish fishery.

The Gulf of Maine northern shrimp fishery has been managed by the Atlantic States Marine Fisheries Commission (ASMFC) since 1972. The ASMFC Northern Shrimp Technical Committee is responsible for providing annual stock assessments and fishery management advice. Previous stock assessments monitored trends in landings, effort, and research vessel survey indices to provide descriptive results and qualitative advice for fishery managers (Clark 1981, 1982; Clark and Anthony 1981). Initiatives were taken in the early 1980s to improve data collection for Gulf of Maine northern shrimp: a port sampling program, which was initiated in the early 1970s to characterize catch, was expanded to all coastal states in the early 1980s, and a state–federal research vessel survey was initiated in 1983 to monitor relative abundance and demographics of northern shrimp. Survey length frequencies were used to estimate mortality using Shepherd's length composition analysis (Terceiro and Idoine 1990) and MULTI-

FAN (Fournier et al. 1991). However, length-based models did not fit the data well because of inter-annual variation in recruitment and growth.

A review of descriptive stock assessment methods and increasing demands by managers for more accurate estimates of stock status suggested that a more quantitative approach was needed to determine whether current levels of exploitation were sustainable (NSTC 1996). We modeled commercial landings data, research vessel survey catches, and life history information to evaluate trends in stock abundance and fishing mortality, characterize the variability of estimates, and estimate levels of relative spawning potential. Quantitative estimates of stock status, with associated uncertainty, and guidance on sustainable harvest rates and stock size levels should substantially improve the information provided to managers of the northern shrimp fishery in the Gulf of Maine.

Data and Methods

Commercial catch.—Annual landings were estimated from seafood dealers' reports (Burns et al. 1983). Landings were sampled monthly since 1984 from each of the three coastal states during the fishing season; 6,000–13,000 length measurements were taken annually. Samples within each year, state, and month were weighted by trip landings. Three percent of total landings from 1984 to

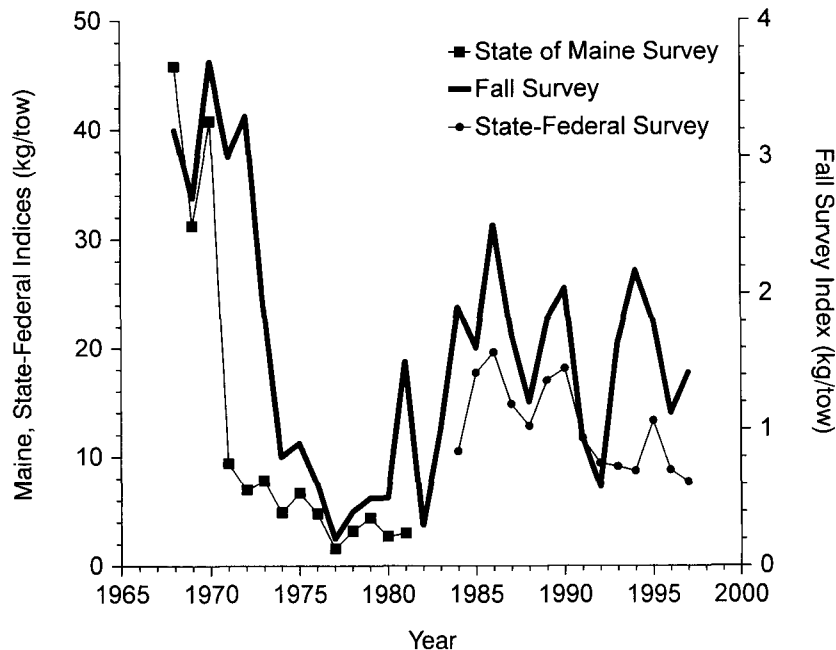


FIGURE 2.—Research vessel survey indices of Gulf of Maine northern shrimp biomass.

1997 were from specific year–state–month strata with no port samples. Mean weight for these landings was estimated by a general linear model of mean weight by year, state, and month. Catch in numbers from 1984 to 1997 was derived as the quotient of landings to mean individual weight by year, state, and month. Catches were also sampled at sea by observers on 393 otter trawl trips targeting northern shrimp from 1984 to 1996.

Research vessel trawl surveys.—Trends in abundance were monitored using data collected by three surveys: (1) the State of Maine survey, (2) the fall bottom trawl survey, and (3) the state–federal survey (Figure 2). The State of Maine survey was conducted during the summer from 1967 to 1981, primarily to collect data on sex and size distribution (Clark 1981, 1982; Clark and Anthony 1981). Fixed stations were sampled with an otter trawl (32-mm cod end mesh) at locations where northern shrimp abundance was historically high. The fall bottom trawl survey has been conducted by the National Marine Fisheries Service (NMFS) since 1963. Stations are sampled with an otter trawl (13-mm cod end mesh) according to a stratified random design (Despres et al. 1988). Although this survey catches relatively fewer northern shrimp and has more measurement error than the other two surveys, it provides a longer time series (data are available for 1968–1997).

The state–federal survey is conducted cooperatively by NMFS and the states of Maine, New Hampshire, and Massachusetts. The survey has been conducted each summer since 1983; it uses a stratified random sampling design (Figure 3) and trawl gear (32-mm cod end mesh) specifically designed for northern shrimp habitat in the Gulf of Maine (Blott et al. 1983; Clark 1989). The state–federal survey is considered to provide the most reliable information available on abundance and size structure. All survey tows that were in the strata used in this assessment caught some northern shrimp (i.e., there were no zero catches in the data set). Statistical distributions of catch per tow (in numbers) from the state–federal survey were positively skewed, and arithmetic stratum means were correlated to stratum variances. Log-transformed catches were more normally distributed, and geometric means were estimated with more precision (annual mean coefficient of variation, $CV = 100 \times SE/\text{mean}$, was 2.4%) than arithmetic means (mean $CV = 13.5\%$). Therefore, relative abundance was estimated using stratified geometric mean catch per tow.

Indices of abundance of several size-based stages were derived from state–federal survey length frequencies using a selectivity method (NEFSC 1995). Selectivity of commercial trawl gear was estimated from a field study conducted

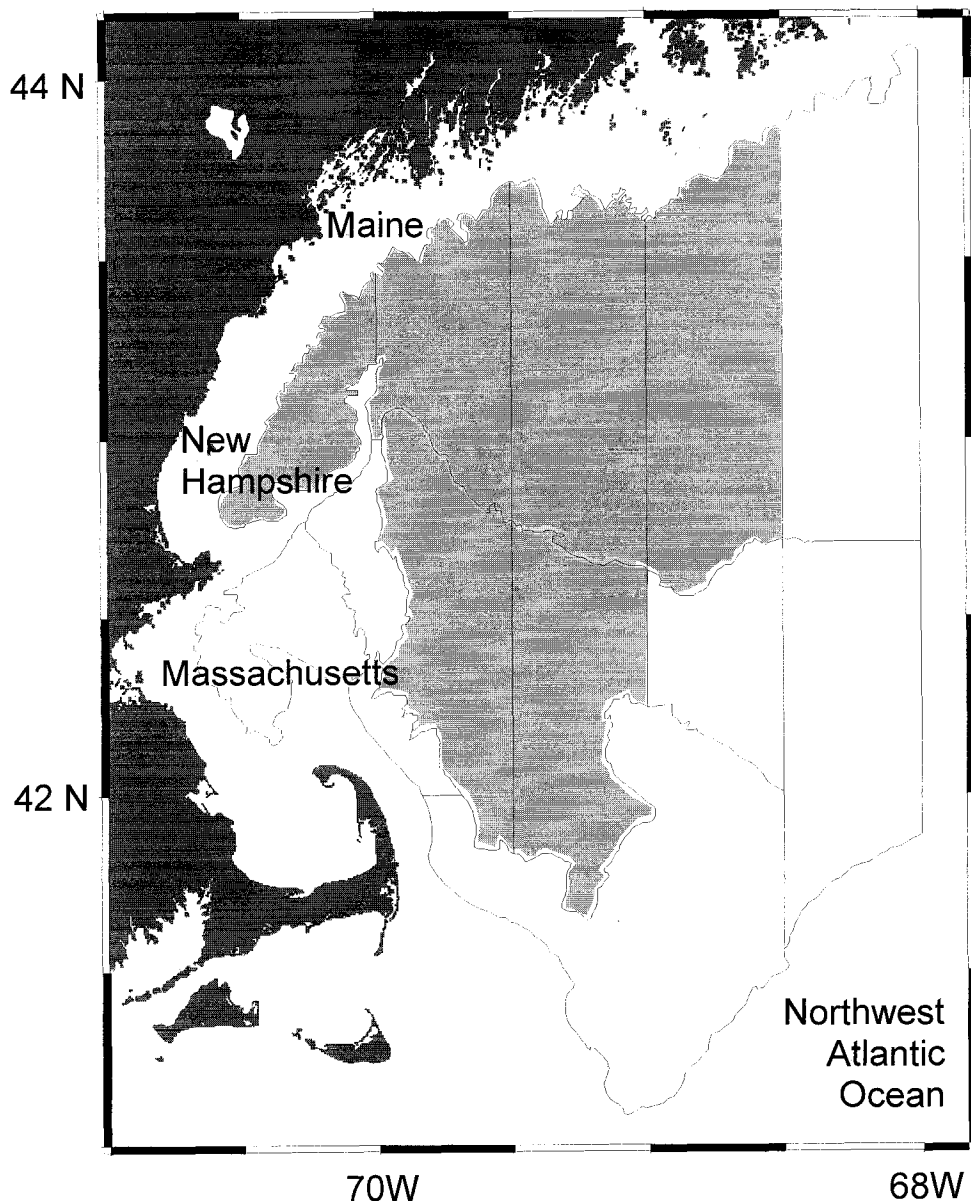


FIGURE 3.—Sampling strata for the state–federal northern shrimp survey. Catches from the lightly shaded strata are included in the stock assessment.

in July 1995 in the western Gulf of Maine (Schick and Brown 1997). The mesh size used in the study (44 mm) has been required by regulation since 1975, and results are similar to those reported by an earlier field study with the same mesh size (Rinaldo et al. 1974). However, some tolerance was allowed in enforcement of minimum mesh sizes for several years after the regulation was enacted (McInnes 1986). Finfish excluder devices, which

have been required since 1992, were found to have little effect on size-selectivity of northern shrimp (Schick and Brown 1997). Results from the field study are assumed to represent the selectivity of commercial trawls during the state–federal survey time series (1985–1997) but may not represent selectivity during earlier years. According to the current selectivity results, vulnerability to the fishery gradually increases with size (e.g., 25% vulnerable

at 19.0 mm carapace length [CL], 50% at 22.5 mm CL, and 75% at 26.0 mm CL; Figure 4).

Number per tow at length from the state-federal survey was partitioned into three components (Figure 4): fully recruited (northern shrimp that are vulnerable to the fishery at the time of the survey), recruits (northern shrimp that will grow to vulnerable size in the next year), and prerecruits (northern shrimp that will not grow to vulnerable size over the next year). The products of selectivity at length (Schick and Brown 1997) and survey catch per tow at length were summed to derive total catch per tow of fully recruited northern shrimp (Figure 4).

The portion of survey catch at length remaining after removing fully recruited northern shrimp (leaving recruits and prerecruits) was then multiplied by end-of-year selectivity at length to obtain an index of recruits (Figure 4). End-of-year selectivity was derived by increasing the carapace length of each interval by 1 year of growth according to a von Bertalanffy growth curve:

$$CL_{t+1} = CL_t + (CL_\infty - CL_t)(1 - e^{-K}), \quad (1)$$

where $CL_\infty = 35.2$ and $K = 0.36$ (McInnes 1986) and calculating the selectivity at CL_{t+1} from selectivity estimates of Schick and Brown (1997). This is mathematically equal to deriving end-of-year selectivity based on end-of-year size frequency with uniform size-classes but is more tractable. We simulated a full year of somatic growth to account for a complete time step from August to July. Catch occurs at approximately midseason (February), but growth from February to July must be included for our definition of recruits because surviving recruits will contribute to our estimate of fully recruited northern shrimp abundance by the next August. Therefore, as a group, recruits are only partially recruited over the entire year (i.e., some grow to recruited size early in the year, and others recruit later in the year). All individuals that grow to recruited size in a given time step must be included as recruits, even if they grow to recruited size after the fishery occurs. Constant growth rates were assumed, because information on interannual variation in growth is not available.

According to this definition of recruitment, age-classes recruit to the fishery over several years, and recruitment in each year is composed of several cohorts. Measuring relative abundance of recruits using gradual selectivity estimates is more realistic than assuming "knife-edged" selectivity

(Collie and Sissenwine 1983) for this fishery and many other trawl fisheries.

Mean weight of recruits and fully recruited northern shrimp were estimated according to length-weight equations from Haynes and Wigley (1969), which were similar to unpublished 1990 survey observations (J. B. O'Gorman, National Marine Fisheries Service, personal communication). Predicted weights were applied to carapace lengths recorded during the survey to represent mean weight at the start of the fishing season (August) and are not affected by the growth adjustment described in equation (1).

Collie-Sissenwine model.—A catch-survey model (C-S; Collie and Sissenwine 1983; Conser and Idoine 1992) was applied to the Gulf of Maine northern shrimp fishery:

$$N_{t+1} = (N_t + R_t - C_t)e^{-M} \quad (2)$$

where t is an annual fishing season (August 1–July 31). Fully recruited abundance at the end of the year (N_{t+1}) are the survivors from fully recruited abundance at the beginning of the year (N_t) plus recruitment (R), minus catch (in numbers, C_t), all reduced by 1 year of natural mortality (e^{-M}).

The instantaneous annual rate of natural mortality (M) was assumed to be 0.25, as approximated from the intercept of a regression of total mortality (Z) on effort (Shumway et al. 1985). An estimate of Z for age-2 and older northern shrimp from State of Maine survey length frequencies was 0.2 from 1977 to 1978, when the fishery was closed (Clark 1981, 1982). These approximations suggest that M for Gulf of Maine northern shrimp is among the lowest levels of M estimated for other northern shrimp stocks in the North Atlantic, which ranged from 0.2 to 0.8 (ICES 1977; Abramson 1981; Frechette and Labonte 1981).

Catch was assumed to be taken 6 months from the time of the state-federal survey (i.e., survey in August and catch in February), which was based on the time of 50% cumulative seasonal catch for 1985–1997:

$$N_{t+1} = [(N_t + R_t)e^{-0.5M} - C_t] e^{-0.5M} \quad (3)$$

so that recruited northern shrimp ($N_t + R_t$) experience a half year of natural mortality ($e^{-0.5M}$), catch is removed, then the survivors from the fishery, $(N_t + R_t)e^{-0.5M} - C_t$, experience another half year of natural mortality.

Abundance is related to state-federal survey indices of relative abundance:

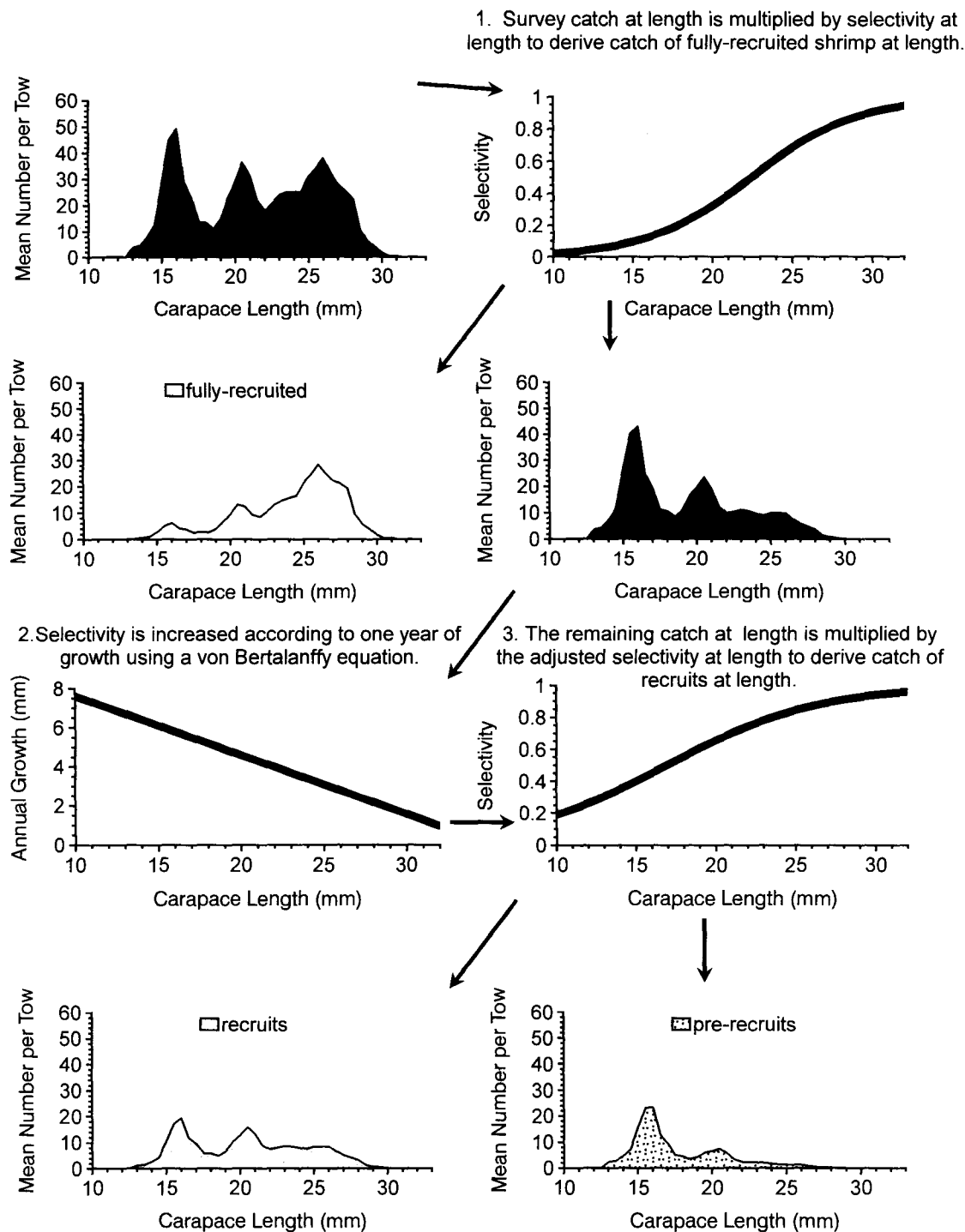


FIGURE 4.—The “selectivity” method of deriving indices of abundance for fully recruited and recruit Gulf of Maine northern shrimp from state–federal survey length distributions. (Example used is 1996.)

TABLE 1.—Summary of input data and results from a Collie–Sissenwine analysis of the Gulf of Maine northern shrimp fishery. Abbreviations are as follows: r = recruit index from the state–federal survey, n = fully recruited index from the state–federal survey, w = mean weight, s_r = selectivity of recruits, R = recruits, N = fully recruited, Z = total mortality, F = fishing mortality, and mt = metric tons.

Fishing year	Input data						Results				
	Survey indices (number/tow)		Mean weight (g)		s_r	Catch (millions)	Abundance (millions)		Z	F	Biomass (mt)
	r	n	w_r	w_n			R	N			
1985	447.6	479.1	8.17	6.40	0.9	352.793	994	954	0.35	0.10	14,147
1986	619.5	925.4	9.39	7.50	0.9	361.171	1,183	1,377	0.54	0.29	21,816
1987	533.4	848.7	10.30	7.18	0.9	425.294	978	1,490	0.68	0.43	22,368
1988	436.3	693.6	10.25	7.25	1.0	228.434	702	1,249	0.71	0.46	17,894
1989	459.9	387.9	8.59	4.88	0.7	283.647	1,192	964	0.43	0.18	14,098
1990	700.7	817.5	8.50	6.63	0.9	442.429	1,324	1,406	0.58	0.33	20,741
1991	511.6	907.7	10.10	8.25	1.0	320.290	836	1,531	0.69	0.44	22,357
1992	374.1	611.9	10.94	6.71	1.0	262.434	613	1,187	0.71	0.46	17,101
1993	313.6	444.4	10.25	6.57	1.0	194.788	516	889	0.67	0.42	12,503
1994	410.0	320.6	8.27	4.65	1.0	270.406	716	719	0.57	0.32	9,273
1995	368.7	364.4	8.29	5.82	0.8	615.318	980	815	0.58	0.33	12,460
1996	485.9	653.1	9.51	6.77	1.0	799.368	887	1,010	0.90	0.65	15,605
1997	257.7	348.6	9.82	6.57	1.0	710.972	535	768	1.10	0.85	11,059
1998	257.4	267.2	9.36	5.40	0.9		524	436			6,907
Mean	441.2	576.4	9.41	6.47	0.9	405.180	856	1,057	0.65	0.40	15,595

$$n_t = q_n N_t e^{\eta_t}, \quad (4)$$

and

$$r_t = q_{r,t} R_t e^{\delta_t}, \quad (5)$$

where r_t and n_t are observed survey indices of recruits and fully recruited northern shrimp, q is catchability of the survey gear, and e^{η_t} and e^{δ_t} are lognormally distributed measurement errors. The process equation is derived by substituting survey indices into equation (3) and including lognormally distributed process error (e^{ϵ_t}):

$$n_{t+1} = [(n_t + r_t/s_{r,t})e^{-0.5M} - q_n C_t] e^{-0.5M} e^{\epsilon_t}, \quad (6)$$

where

$$s_{r,t} = q_{r,t}/q_n \quad (7)$$

is the relative selectivity of recruits to fully recruited northern shrimp in year t .

Selectivity studies (Blott et al. 1983) and survey catch at length suggest that age-1.5 northern shrimp are sampled less efficiently than age-2 and older northern shrimp, because total catch per tow is greater at age-2.5 than at age-1.5 for some cohorts. There are two components to survey selectivity of age-1.5 northern shrimp: the 32-mm cod end mesh in the survey trawl may not retain some small northern shrimp; and in some years, age-1.5 males may not completely migrate from inshore areas to the survey strata (which are offshore; Figure 3). For the present analysis, s_r was approxi-

mated from the relative sampling efficiency of northern shrimp smaller than 19 mm CL to that of larger northern shrimp and the relative proportions of those sizes constituting total recruits and fully recruited indices.

The parameters n_t , r_t , and q_n were estimated by nonlinear least squares of log survey measurement errors (equations 4, 5) and process errors (from equation 6) for the entire time series. Abundance of recruits in 1998 was not directly estimated, but calculated from equation (5) without measurement error. Process error is measured as the difference between predicted n_t (equation 4) and calculated n_t (equation 5). Biomass was derived as the product of abundance and mean weight (Table 1).

The instantaneous annual total mortality rate (Z) and instantaneous annual fishing mortality rate (F) were calculated from abundance estimates:

$$Z_t = \log_e[(N_t + R_t)/N_{t+1}] \quad (8)$$

and

$$F_t = Z_t - M. \quad (9)$$

Vulnerability to the fishery is influenced by physical selectivity of fishing gear and the available sizes of northern shrimp. Based on movement patterns of young males and ovigerous females (Haynes and Wigley 1969; Shumway et al. 1985), seasonal and spatial changes in fishing behavior are likely to influence the effective vulnerability at size of northern shrimp to the fishery. However,

as described above, we defined recruits as those northern shrimp that will grow to a selected size by the end of the year. If fishing behavior can be controlled to avoid areas and times in which small northern shrimp are available, survival of recruits (as we define them) will be high and the aggregate F on recruits and fully recruited northern shrimp will be lower than F on the fully recruited component of northern shrimp (as shown in equation 8).

Variability of C-S estimates was assessed using conditional bootstrap analysis (Efron 1979). One thousand bootstrapped estimates of n_t , r_t , and q_t were derived by randomly resampling log errors (from equations 4–6). Minimum confidence limits were approximated using percentiles of bootstrap estimates (Efron 1979).

Sensitivity of C-S results to several model assumptions was evaluated by comparing alternative model runs. Sensitivity analyses were performed with several alternative assumptions: M ($M = 0.35$; M was 0.25 in the base run); constant s_r (relative vulnerability of recruits to the survey gear; three alternative runs for $s_r = 0.7$, $s_r = 0.9$, $s_r = 1.0$; variable s_r [0.7–0.9] was assumed in the base run); statistical weighting (process error weight = $2 \times$ observation error weight; the base run assumed equal weighting); transformation of survey catches (r_t and n_t were derived from arithmetic mean catch per tow; the base run derived r_t and n_t from geometric mean catch per tow); and survey indices based on different fishery selectivity at length (ratios of cumulative length frequencies from the fishery and the spring groundfish survey which produced similar length at 50% selectivity and a much steeper curve than the selectivity ogive used to derive r_t and n_t in the base run).

The C-S model does not have the same convergence properties as virtual population analysis (VPA), in which estimates of initial stock size improve as more ages of a cohort are included in the analysis. However, subterminal C-S estimates (i.e., estimates in the second year through the penultimate year) are generally more reliable than terminal estimates (i.e., estimates in the first or last year), because subterminal estimates of n_t contribute to two process errors in the objective function (as n_t , then as n_{t+1} ; equation 6), whereas terminal estimates of n_t contribute to a single process error. Therefore, similar to VPA, retrospective analysis can be used to test the general consistency of terminal estimates by comparing subterminal estimates to retrospective terminal estimates (Sinclair

et al. 1990). Retrospective analysis was performed by sequentially truncating the last year of catch and survey data from the analysis and reestimating the parameters. Results from nine retrospective C-S analyses (based on 1985–1996 catch data, 1985–1995 catch data, etc.) were compared to the base run, described above, to investigate the stability of estimates in the last year of the analysis and the possibility that terminal mortality estimates are systematically inconsistent. The general magnitude of retrospective differences was measured by root mean square difference (Cadrin and Vaughan 1997).

Surplus production model.—An alternative method of estimating stock size and F was conducted for comparison to results from C-S analysis. A nonequilibrium surplus production model (ASPIC; Prager 1994, 1995) was fit to total catch and survey biomass indices from the 1968–1997 fishing seasons. The model assumes logistic population growth, in which the change in stock biomass over time (dB_t/dt) is a quadratic function of biomass (B):

$$dB_t/dt = rB_t - (r/K)B_t^2, \quad (10)$$

where r is the instantaneous annual growth rate, and K is the carrying capacity. For a fished stock, the rate of change is reduced by yield (Y , in units of biomass):

$$dB_t/dt = rB_t - (r/K)B_t^2 - Y_t. \quad (11)$$

Relative biomass indices from the State of Maine survey, the fall bottom trawl survey, and the state-federal survey were used to calibrate the predicted biomass trajectory. Similar to the C-S model, biomass is related to survey indices of relative biomass:

$$b_t = q_t B_t e^{B_t}, \quad (12)$$

where b_t is an observed survey index of biomass, q_t is the catchability of the i^{th} survey, and e^{B_t} is a lognormally distributed measurement error.

Biomass in 1968 (B_1), r , K , q_{fall} , q_{Maine} , and $q_{\text{S-F}}$ (q for fall, Maine, and state-federal) were estimated by nonlinear least squares of log survey measurement errors. Note that no assumption about M is needed for the surplus production analysis. Log survey measurement errors were randomly resampled 1,000 times for bootstrap estimates of precision.

Two alternative production model runs were investigated. The first sensitivity run excluded the state-federal survey to provide a more indepen-

dent confirmation of the C-S analysis. Another alternative run excluded both the state-federal survey and State of Maine survey.

Yield and eggs per recruit model.—Yield per recruit (Thompson and Bell 1934) and percent maximum spawning potential (Gabriel et al. 1989; Goodyear 1993) were estimated for the Gulf of Maine northern shrimp fishery. For these dynamic pool methods, "recruit" refers to recruitment to the population (a newly hatched individual), whereas it refers to recruitment to the fishery in the C-S model. Yield and egg production were derived as a function of abundance at the time of hatching (approximately February 1) to reflect size and weight at age during larval release and the fishery. The model assumes that annual growth and protandrous transition occur before oviposition and the onset of the fishing season. Length at age was estimated using von Bertalanffy growth parameters ($L_{\infty} = 35.2$ mm, $K = 0.36$, $t_0 = 0.06$; McInnes 1986). Selectivity at size was estimated using the selectivity curve described above (Schick and Brown 1997, without the adjustment for a year of growth). Mean weight at length for males and females was estimated using relationships reported by Haynes and Wigley (1969). Batch fecundity was estimated by a linear relationship to carapace length (Shumway et al. 1985).

Proportion female at the time of hatch was estimated by the average of 1984–1997 observed sex ratios at length from the state-federal survey applied to a carapace length which was increased by a half year of growth using equation (1). Sex ratios at length can be variable and compensatory (protandrous transition can be accelerated at low stock size and delayed for extremely abundant cohorts). However, during 1984–1997, size at transition was relatively stable. The implications of compensatory maturation are that our analysis may underestimate egg production at low abundance (high F) and overestimated egg production at high abundance (low F). However, the degree of potential compensation is not known, and assuming a constant maturity schedule is more risk averse than incorporating compensation.

As described above, M was assumed to be 0.25 (Shumway et al. 1985). Anthony (1982) offers the rule of thumb that dynamic pool models should be simulated to a maximum age at which 5% of the initial cohort abundance survives with no fishing (this rule of thumb can also be expressed as maximum age = $3/M$; Gabriel et al. 1989). For example, yield and egg production for a stock with a lifetime M of 0.25 should be simulated through

age-12. However, there appears to be a disparity between published estimates of life span and the estimate of M for northern shrimp sampled in the Gulf of Maine fishery and research surveys (Clark 1981, 1982; Shumway et al. 1985). Haynes and Wigley (1969) inspected length distributions and ontogenetic stages of samples collected from 1963 to 1965, when harvest levels were relatively low, and concluded that few northern shrimp lived to be older than age 5. We simulated yield and egg production through age 7, assuming no survival to age 8. However, two alternative analyses were conducted to assess the sensitivity of results to this assumption: the first sensitivity analysis simulated yield and egg production to age 12, and the other simulated an increase in M after spawning (as suggested by Haynes and Wigley 1969). An additional analysis was conducted assuming a historical estimate of selectivity with 38-mm mesh (northern shrimp are 25% vulnerable at 12 mm CL, 50% vulnerable at 14 mm oblique CL, and 75% vulnerable at 16 mm CL; Rinaldo et al. 1974) to approximate historical levels of egg production.

Results

Annual landings increased from less than 300 metric tons (mt) before 1964 to a peak of 12,100 mt during the 1969 season (August 1968–July 1969; Figure 1). After 1972, landings declined rapidly, and the fishery was closed in 1978. The fishery reopened in 1979, and seasonal landings increased gradually to an annual average of 3,100 mt from 1981 to 1994. Landings increased to 6,500 mt in 1995 and to 9,200 mt in 1996, then decreased slightly to 7,100 mt in 1997. Maine landings constituted 75% of total landings from 1984 to 1997, and New Hampshire and Massachusetts landed 8% and 17%, respectively.

The size of landed northern shrimp generally increased from December to January, peaked in February, and decreased through the spring. This pattern reflects shifts in distribution of fishing effort in response to seasonal movements of mature females: inshore in early winter and offshore after their eggs hatch.

Sea sampling observations indicate that weight of discarded northern shrimp was less than 1% of total northern shrimp catch in all years. Discarded northern shrimp were not sampled for information on size distribution. Therefore, discarded catch was considered negligible and was not included in the present analyses.

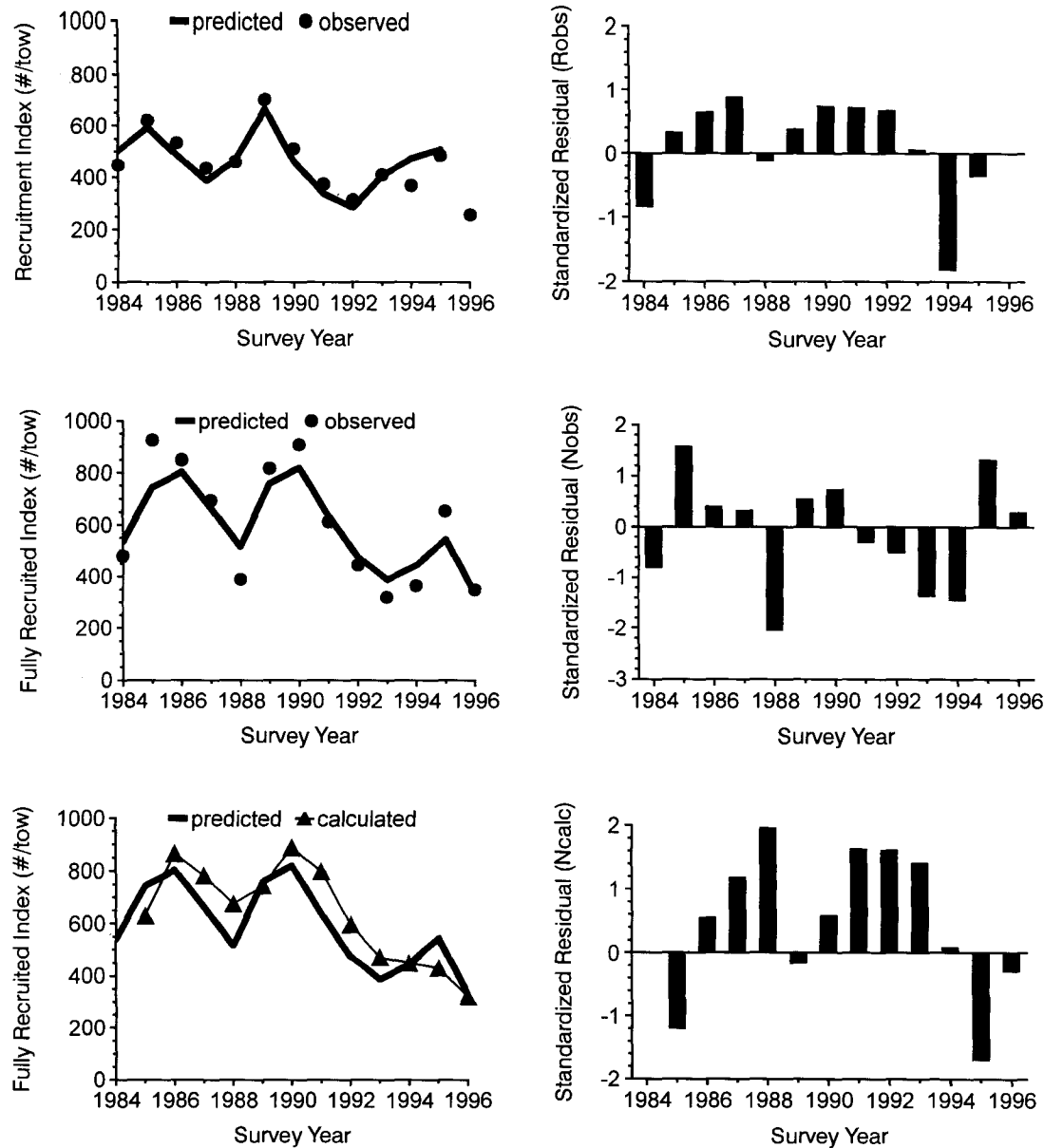


FIGURE 5.—Summary of results from a Collie-Sissenwine analysis of the Gulf of Maine northern shrimp fishery (#/tow: mean number per tow; Robs: observation error of recruitment index; Nobs: observation error of full-recruited index; Ncalc: process error of calculated fully recruited abundance).

Collie-Sissenwine Model

The state-federal survey index of recruitment peaked in 1985, 1989, and 1995, but the 1997 survey index was the lowest in the time series (Figure 5). Survey indices of fully recruited abundance reflected the recruitment series with high levels during 1985–1987 and 1989–1991, but the 1997 index declined to a low level (Figure 5).

The C-S model parameters appear to have been relatively well estimated. Relative standard errors for fully recruited abundance estimates (in original units) ranged from 19% to 25%; estimates of recruitment were slightly less precise (CV = 25–27%), and q_n was estimated with moderate precision (CV = 20%). There were no large correlations ($|r| < 0.4$) among the 26 parameter esti-

mates. Standardized residuals of the observation errors (equations 4, 5) and process errors (equation 6) ranged from -2.03 to 1.95 without significant annual patterns, indicating that the model fits the data well.

Abundance and biomass estimates correspond to the August 1 start of the fishing season (Table 1). Therefore, the pattern of survey recruitment indices from the summer are generally reflected in the estimate of recruitment for the following fishing season. Recruitment estimates averaged 0.9 billion from 1985 to 1998, peaked at 1.3 billion in 1990, but then decreased to 0.5 billion in 1997 and 1998 (Table 1). Fully recruited abundance estimates averaged 1.1 billion over the C–S time series, peaked at 1.5 billion in 1991, and then decreased to 0.4 billion in 1998, the lowest level in the time series. Estimates of total stock biomass averaged 15,600 mt from 1985 to 1998, peaked at over 22,000 mt in 1987 and 1991, but decreased to 6,900 mt in 1998. Annual estimates of F averaged 0.34 from 1985 to 1995 and increased to 0.65 in 1996 and to 0.85 in 1997. Total mortality estimates were within the range of length-based analyses for the same period (Terceiro and Idoine 1990; Fournier et al. 1991).

Bootstrap results suggest that estimates of abundance and mortality were relatively precise (Figure 6). Bootstrap estimates of total stock biomass at the beginning of the 1998 fishing season averaged 6,900 mt, with an 80% confidence interval of 5,000–8,400 mt. The distribution of bootstrap biomass estimates were skewed to the right (Figure 6), which is consistent with the assumed lognormal error structure. The mean bootstrapped value of 1997 F was 0.85, with an 80% confidence interval of 0.64–1.05.

All sensitivity analyses produced similar diagnostics and estimates of total mortality, both in magnitude (e.g., average total mortality was 0.7 for the entire time series) and temporal pattern (e.g., mortality estimates from all model runs peaked in 1997). All alternative estimates of abundance and mortality were strongly correlated with those reported in Table 1 ($r = 0.70$ for untransformed survey data, $r > 0.96$ for all other sensitivity analyses). These sensitivity results are consistent with C–S sensitivity analyses reported by Collie and Kruse (1998): q estimates increased with greater values of M ; results were very similar within an s_r range of 0.7–1.0; and q estimates increased with greater process error weight (evaluating the sensitivity of results to decreased weighting of process error was not tested, because pro-

cess error accounted for 50% of total variance for the base run with equal weighting). The analysis based on nontransformed survey data produced similar estimates of abundance and F to the run based on transformed survey data because the greater survey indices produced a greater estimate of q , and the analysis that assumed alternative selectivity estimates had very similar results to those using the experimental estimates of selectivity. It appears that the level and temporal pattern of mortality estimates are robust to the assumptions which were evaluated.

Retrospective analysis showed that terminal mortality estimates were relatively consistent in most years. Retrospective differences in Z were positive for the first two terminal estimates (1988 and 1989), negative for the next three (1990–1992), and positive for the last four (1993–1996). The root mean square retrospective difference of terminal Z estimates was 0.12.

Model results reflect the recent intensification of the fishery and declines in survey vessel catches. It appears that the high F in 1996 and 1997 resulted from large removals from low stock sizes. The retrospective analysis indicated that terminal F estimates in recent years were greater than revised estimates, which suggests that F for 1997 may be overestimated. However, even liberal interpretation of C–S model results leads to the conclusion that F was high in the most recent years: 90% of the bootstrap estimates of mean F for 1996–1997 (the 2-year mean, which is less sensitive to terminal abundance estimates) were greater than 0.61.

Surplus Production Model

The biomass index from the State of Maine survey began declining in 1968 and reflects the stock collapse of the late 1970s (Clark 1981, 1982). The fall bottom trawl survey indicates a 95% decrease in biomass from the late 1960s to the late 1970s. The index subsequently increased in the 1980s and has since fluctuated at approximately 40% of levels from the late 1960s. Survey indices of stock biomass were moderately correlated ($r = 0.7$ between the State of Maine and fall bottom trawl surveys, and $r = 0.5$ between the fall bottom trawl and state–federal surveys). The majority of variance in the fall bottom trawl and State of Maine surveys was explained by the model ($R^2 = 0.7$ and 0.6 , respectively), but none of the variation in the state–federal survey was resolved ($R^2 = 0.0$; Figure 7). However, the predicted series of biomass during the state–federal time series is relatively

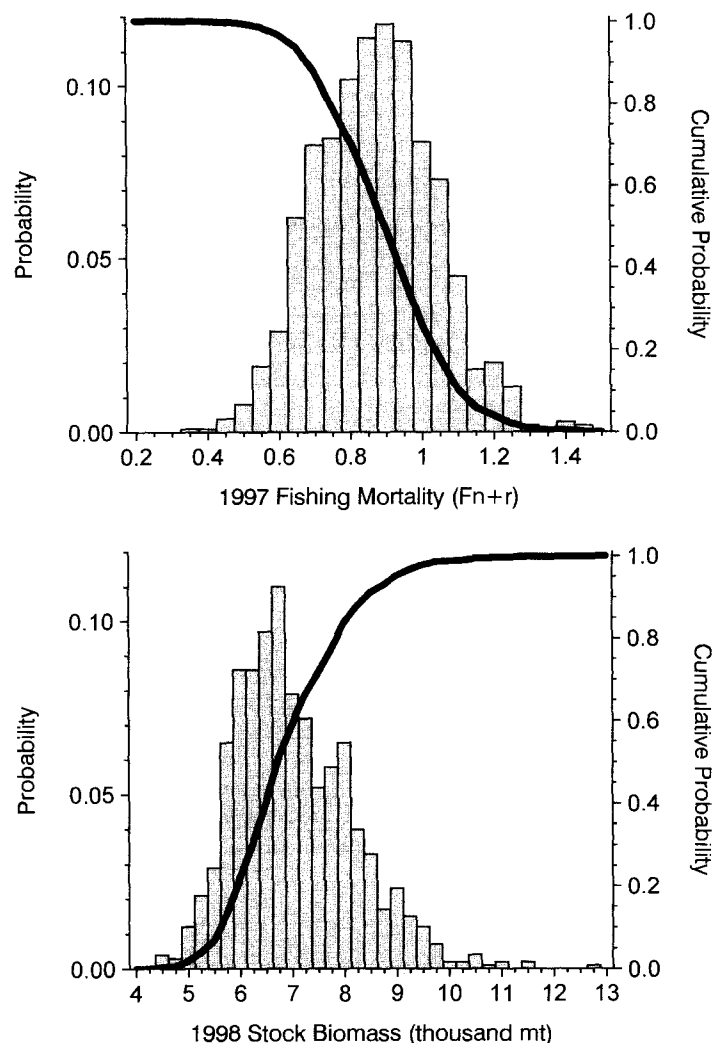


FIGURE 6.—Bootstrap estimates of 1997 fishing mortality and 1998 stock biomass from Collie–Sissenwine analysis of Gulf of Maine northern shrimp.

constant, and none of the variance in the fall bottom trawl survey during 1984–1997 is explained by the model ($R^2 = 0$; i.e., the mean explains as much variance in the survey as the model prediction).

The production model could not account for the distinct recent recruitment events, which were apparent from the state–federal survey and the size structure of landings, because the production model assumes a generalized level of recruitment as a function of stock biomass, and survey indices of recruitment are not considered in the model. The result of ignoring recruitment signals is that patterns of biomass from the state–federal survey were interpreted as observation error and little

variance was explained. Therefore, biomass estimates in any single year should be suspect. However, estimates of F from the biomass dynamics model generally confirm the pattern and magnitude of estimates from the C–S model (Table 2; Figure 8).

Biomass estimates exceeded 40,000 mt in the late 1960s, gradually decreased to less than 5,000 mt in the late 1970s, increased to a stable average of 15,000 mt from 1984 to 1996, then decreased to 7,000 mt in 1998. Although selectivity changed as a result of regulated mesh sizes, ASPIC results are generally robust to moderate changes in selectivity (Prager et al. 1996).

Bootstrap results suggest that B_1 , r , K and q were estimated with moderate precision (relative inter-

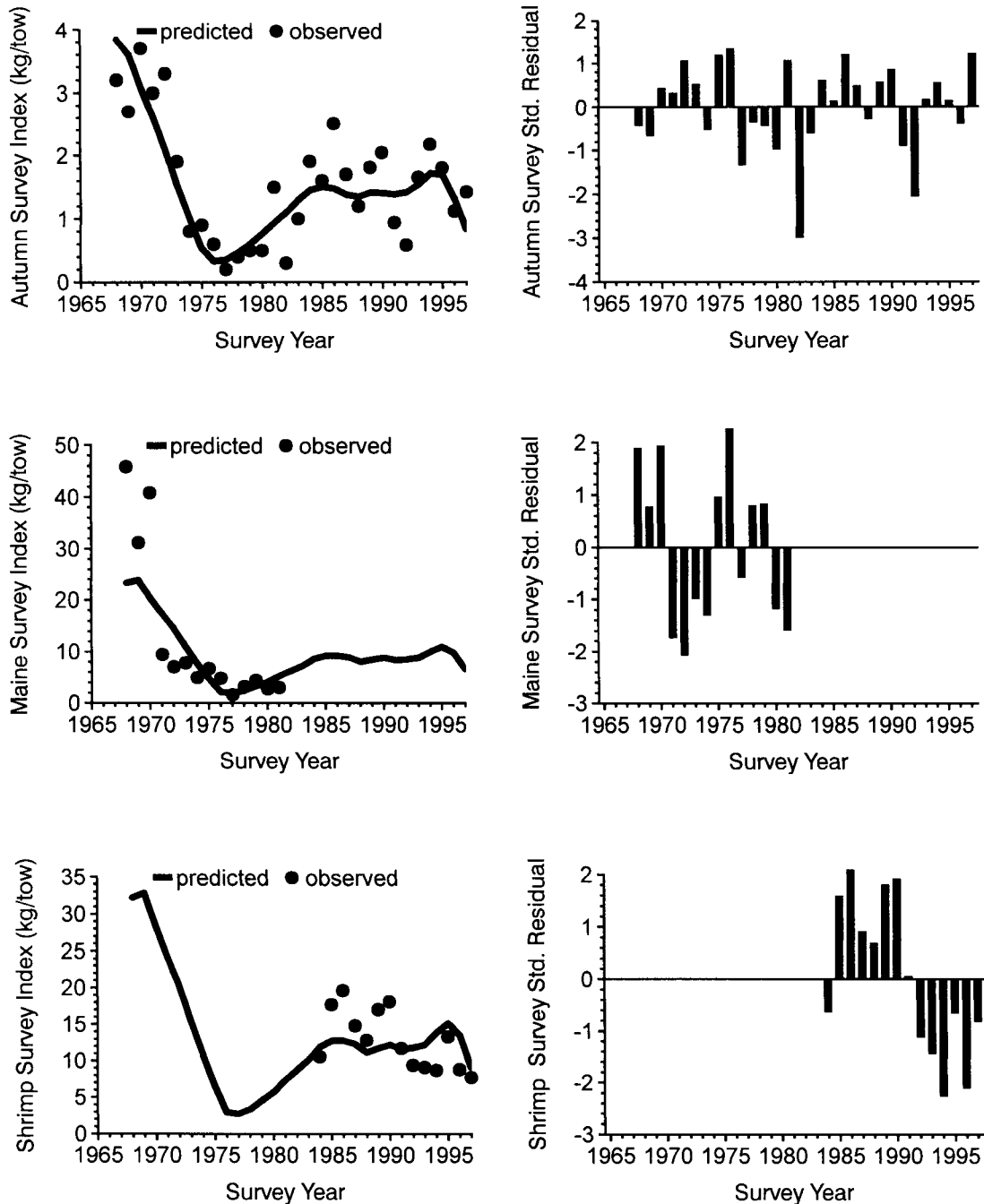


FIGURE 7.—Summary of results from a surplus production analysis of the Gulf of Maine northern shrimp fishery.

quartile ranges were 15–25%). Estimates of biomass and F appear to be more variable than those from the C–S model. The approximate 80% confidence intervals were 3,000–12,000 mt for 1998

biomass and 0.5–1.4 for 1997 F . The distribution of bootstrap biomass estimates were skewed to the right, which is consistent with the assumed log-normal error structure.

TABLE 2.—Summary of input data and results from a surplus production analysis of the Gulf of Maine northern shrimp fishery; F = fishing mortality; mt = metric tons.

Year	Input data			Results	
	Survey indices (kg/tow)		Catch (mt, thousands)	Bio- mass (mt, thou- sands)	F
	Fall	Maine			
1968	3.2	45.8		a	a
1969	2.7	31.2	12.140	a	a
1970	3.7	40.8	11.330	a	a
1971	3.0	9.4	10.590	a	a
1972	3.3	7.0	11.220	24	0.5
1973	1.9	7.8	9.691	18	0.6
1974	0.8	4.9	8.024	13	0.8
1975	0.9	6.7	6.142	8	1.1
1976	0.6	4.8	1.387	3	0.4
1977	0.2	1.6	372	3	0.1
1978	0.4	3.2	17	4	0.0
1979	0.5	4.4	487	5	0.1
1980	0.5	2.7	339	6	0.0
1981	1.5	3.0	1.071	8	0.1
1982	0.3		1.530	10	0.1
1983	1.0		1.397	12	0.1
1984	1.9		2.951	14	0.2
1985	1.6		4.131	15	0.3
1986	2.5		4.635	15	0.3
1987	1.7		5.253	14	0.4
1988	1.2		3.031	13	0.2
1989	1.8		3.315	14	0.2
1990	2.0		4.662	14	0.3
1991	0.9		3.571	14	0.2
1992	0.6		3.444	14	0.2
1993	1.7		2.143	15	0.1
1994	2.2		2.915	17	0.2
1995	1.8		6.466	18	0.4
1996	1.1		9.166	16	0.7
1997	1.4		7.079	11	0.8
1998				7	
Mean	1.6	12.4	4.807	12	0.3

^a Results for the first several years in the time series are not reliable (Prager 1994, 1995).

The alternative production model without the state-federal survey had very similar parameter estimates and predicted trajectories of F and biomass (8,000 mt in 1998). The other sensitivity analysis, with only the fall survey, did not converge well but produced similar parameter estimates and slightly lower biomass trajectories (7,000 mt in 1998). Predicted biomass trajectories from the two alternative runs were highly correlated to the results reported in Table 2 ($r > 0.99$).

Yield and Eggs per Recruit

Maximum yield per recruit was 4.2 g at $F = 0.77$ (F_{\max}) (Table 3; Figure 9). The increase in yield per unit F decreased to one tenth the initial increase at $F = 0.46$ ($F_{0.1}$). Maximum spawning potential (i.e., with no F) was 2,400 eggs per re-

cruit. Spawning potential was reduced by half at $F = 0.25$ ($F_{50\%}$).

An alternative analysis which simulated survival to age 12 produced slightly greater estimates of maximum yield per recruit (4.4 g) and maximum eggs per recruit (2,700) and lower F reference points ($F_{\max} = 0.61$; $F_{0.1} = 0.31$; $F_{50\%} = 0.17$) than the results above (that simulated survival to age 7).

An exploratory analysis which assumed that M increased to 0.5 after spawning produced slightly lower estimates of yield per recruit (4.1 g), substantially lower estimates of maximum eggs per recruit (1,800) and greater F reference points ($F_{\max} = 0.89$; $F_{0.1} = 0.52$; $F_{50\%} = 0.28$) than results from assuming $M = 0.25$ to age 7. However, reliable estimates of postspawn mortality are not available, and these sensitivity results are merely exploratory.

The alternative analysis that assumed a historical selectivity pattern produced a much lower estimate of maximum yield per recruit (3.4 g) and substantially lower reference points ($F_{\max} = 0.43$; $F_{0.1} = 0.29$; $F_{50\%} = 0.15$).

Discussion

The Collie-Sissenwine model fit the data well and appears to provide reliable estimates of stock size and F . Our modeling efforts clearly benefited from the strong corresponding signals in catch and stock size, which result from intense port sampling and well-designed research vessel surveys. This quantitative stock assessment for the Gulf of Maine northern shrimp stock appears to be an improvement over descriptive methods and provides an objective basis for fishery management. In 1996, a descriptive synthesis of catch and survey data concluded, "short term commercial prospects are favorable, because abundance is relatively high" (NSTC 1996). A revised assessment of the same information that used the present methods concluded, "the stock is at a below-average level of biomass and F is high" (NEFSC 1997). In retrospect, the quantitative methods provided a more accurate assessment of stock status: under similar management restrictions, 1997 landings and survey indices substantially decreased; and a preliminary estimate of 1998 landings is even lower (approximately 4,000 mt). The same methods, updated here through 1997, suggest that the levels of F estimated for 1996 (and 1997) were significantly greater than sustainable levels. Both C-S and ASPIC modeled temporal patterns in stock size (as indexed by survey catches) according to

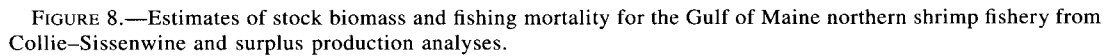


TABLE 3.—Summary of input data for a yield and eggs-per-recruit analysis of the Gulf of Maine northern shrimp fishery and results for an example fishing mortality of 0.2 and 1,000 age-0 recruits; M = natural mortality, F = fishing mortality, and S = selectivity to fishery.

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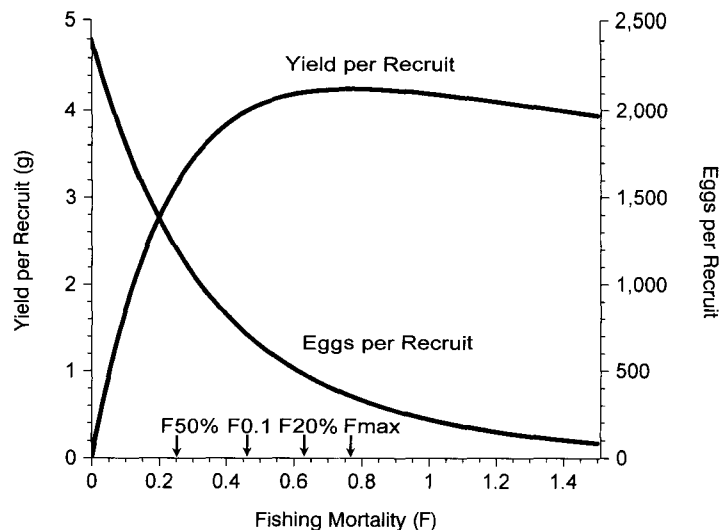


FIGURE 9.—Yield and egg production per recruit for the Gulf of Maine northern shrimp fishery.

expected responses to fishery removals by assuming simple population dynamics. Although assessing stock status without such formalized models can be difficult and subjective, descriptive methods are common for assessing the status of northern shrimp stocks (Hvingel 1997). The present quantitative methods, particularly the use of gradual selectivity for C-S analysis, may perform well for other fish stocks with unavailable or unreliable information on age structure.

Egg-per-recruit reference points are appropriate management targets for Gulf of Maine northern shrimp because there appears to be a strong spawner-recruit relationship, and low levels of spawning potential increase the risk of poor recruitment. Reproductive success for Gulf of Maine northern shrimp is a function of population fecundity and spring seawater temperature (Richards et al. 1996), and landings are correlated to lagged population fecundity (Stickney 1980; Richards et al. 1996).

Information from the stock collapse in the 1970s may provide guidance on the level of sustainable F for Gulf of Maine northern shrimp. Biomass indices from the Maine survey and the biomass dynamics model suggest that biomass began to decline in 1968. Clark and Anthony's (1980) estimates of F from survey length frequencies were 0.69–0.75 from 1968 to 1970. Estimates of F for 1973–1975 from the production model ranged from 0.6 to 1.1. According to the egg-per-recruit analysis that assumed historical selectivity, spawning potential was reduced to less than 10% of maximum when F exceeded 0.6. It appears that the

stock was not replacing itself in the late 1960s and early 1970s, and the stock collapsed when egg production was reduced further. In the absence of more reliable stock-recruitment information, $F_{20\%}$ would be a precautionary overfishing threshold (Goodyear 1993), which would result in target F s well below 0.6 under the current exploitation pattern (Figure 9). Stock sizes were relatively stable from 1985 to 1995, when annual F averaged 0.34. An F of 0.34, which corresponds to 40% of maximum egg production per recruit, may be an appropriate ad hoc management target.

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References

- Abramson, N. 1981. Current stock assessment panel. Pages 259–275 in T. Frady, editor. Proceedings of

- the international pandalid shrimp symposium. University of Alaska, Sea Grant Report 81-3, Fairbanks.
- Anthony, V. C. 1982. The calculation of $F_{0.1}$: a plea for standardization. Northwest Atlantic Fisheries Organization, Scientific Council Report 82/VI/64, Dartmouth, Nova Scotia.
- Apollonio, S., D. K. Stevenson, and E. E. Dunton, Jr. 1984. Effects of temperature on the biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. Maine Department of Marine Resources, Reference Document 83/30, West Boothbay Harbor.
- Blott, A. J., P. J. Diodati, S. H. Clark, D. B. Sampson, and D. F. Schick. 1983. Development of a new research trawl for northern shrimp, *Pandalus borealis*, in the Gulf of Maine. International Council for the Exploration of the Sea, C. M. 1983/B:21, Copenhagen.
- Burns, T. S. R., R. Schultz, and B. E. Brown. 1983. The commercial catch sampling program in the northeastern United States. Canadian Special Publication of Fisheries and Aquatic Sciences 66:82-95.
- Cadrin, S. X., and D. S. Vaughan. 1997. Retrospective analysis of virtual population estimates for Atlantic menhaden stock assessment. Fishery Bulletin 95: 445-455.
- Clark, S. H. 1981. Recent trends in the Gulf of Maine northern shrimp fishery. North Atlantic Fisheries Organization, Scientific Council Report Document 81/XI/148, Dartmouth, Nova Scotia.
- Clark, S. H. 1982. Assessment and management of the Gulf of Maine northern shrimp (*Pandalus borealis*) fishery. International Council for the Exploration of the Sea, C. M. 1982/K:13, Copenhagen.
- Clark, S. H. 1989. State-federal northern shrimp survey. Pages 27-2 in T. R. Azarovitz, J. McGurrin, and R. Seagraves, editors. Proceedings of a workshop on bottom trawl surveys. Atlantic States Marine Fisheries Commission, Special Report 17, Washington, D.C.
- Clark, S. H., and V. C. Anthony. 1981. An assessment of the Gulf of Maine northern shrimp resource. Pages 207-224 in T. Frady, editor. Proceedings of the international pandalid shrimp symposium. University of Alaska, Sea Grant Report 81-3, Fairbanks.
- Collie, J. S., and G. H. Kruse. 1998. Estimating king crab (*Paralithodes camtschaticus*) abundance from commercial catch and research survey data. Canadian Special Publication of Fisheries and Aquatic Sciences 125:73-83.
- Collie, J. S., and M. P. Sissenwine. 1983. Estimating population size from relative abundance data measured with error. Canadian Journal of Fisheries and Aquatic Sciences 40:1871-1879.
- Conser, R. J., and J. Idoine. 1992. A modified DeLury model for estimating mortality rates and stock sizes of American lobster populations. Northeast Fisheries Science Center, Stock Assessment Workshop 14/7, Reference Document, Woods Hole, Massachusetts.
- Despres, L. I., T. R. Azarovitz, and C. J. Byrne. 1988. Twenty-five years of fish surveys in the northwest Atlantic: the NMFS Northeast Fisheries Center's bottom trawl survey program. Marine Fisheries Review 50(4):69-71.
- Dow, R. L. 1977. Effects of climate cycles on the relative abundance and availability of commercial marine and estuarine species. Journal du Conseil Conseil International pour l'Exploration de la Mer 37: 274-280.
- Efron, B. 1979. Bootstrap methods: another look at the jackknife. Annals of Statistics 7:1-26.
- Fournier, D. A., J. R. Sibert, and M. Terceiro. 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method. Canadian Journal of Fisheries and Aquatic Sciences 48:591-598.
- Frechette, J., and S. S. M. Labonte. 1981. Biomass estimate, year-class abundance and mortality rates of *Pandalus borealis* in the northwest Gulf of St. Lawrence. Pages 307-330 in T. Frady, editor. Proceedings of the international pandalid shrimp symposium. University of Alaska, Sea Grant Report 81-3, Fairbanks.
- Gabriel, W. L., M. P. Sissenwine, and W. J. Overholtz. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. North American Journal of Fisheries Management 9:383-391.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. Canadian Special Publication of Fisheries and Aquatic Sciences 120:67-81.
- Haynes, E. B., and R. L. Wigley. 1969. Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. Transactions of the American Fisheries Society 98:60-76.
- Hvingel, C., editor. 1997. Northern shrimp research in the North Atlantic—state of the art and future research strategy. TemaNord 1997. (Nordic Council of Ministers, Copenhagen.)
- ICES (International Council for the Exploration of the Sea). 1977. Report of the working group on assessment of *Pandalus borealis* stocks. International Council for the Exploration of the Sea, C. M. 1977/K:10, Copenhagen.
- McInnes, D. 1986. Interstate fishery management plan for the northern shrimp (*Pandalus borealis* Kroyer) fishery in the western Gulf of Maine. Atlantic States Marine Fisheries Commission, Fisheries Management Report 9, Washington, D.C.
- NEFSC (Northeast Fisheries Science Center). 1995. Sea scallop in mid-Atlantic and Georges Bank. Pages 97-155 in Report of the 20th northeast stock assessment workshop. Northeast Fisheries Science Center, Reference Document 95-18, Woods Hole, Massachusetts.
- NEFSC (Northeast Fisheries Science Center). 1997. Northern shrimp advisory report. Pages 22-24 in 25th northeast regional stock assessment workshop. Northeast Fisheries Science Center, Reference Document 97-15, Woods Hole, Massachusetts.
- NMFS (National Marine Fisheries Service). 1997. Fish-

- eries of the United States, 1996. NMFS Current Fishery Statistics 9600.
- NSTC (Northern Shrimp Technical Committee). 1996. Assessment report for Gulf of Maine northern shrimp. Atlantic States Marine Fisheries Commission, Washington, D.C.
- Prager, M. H. 1994. A suite of extensions to a non-equilibrium surplus-production model. *Fishery Bulletin* 92:374–389.
- Prager, M. H. 1995. User's manual for ASPIC: a stock-production model incorporating covariates. Southeast Fisheries Science Center, Miami Laboratory, Document MIA-92/93-55, Miami.
- Prager, M. H., C. P. Goodyear, and G. P. Scott. 1996. Application of a surplus production model to a swordfish-like simulated stock with time-changing gear selectivity. *Transactions of the American Fisheries Society* 125:729–740.
- Richards, A., M. Fogarty, S. Clark, D. Schick, P. Diodati, and B. O'Gorman. 1996. Relative influence of reproductive capacity and temperature on recruitment of *Pandalus borealis* in the Gulf of Maine. International Council for the Exploration of the Sea, C. M. 1996/K:13, Copenhagen.
- Rinaldo, R. G., B. E. Barrett, D. B. MacIssac, K. Smith, and P. D. Colosi. 1974. Northern shrimp gear evaluation study. Atlantic States Marine Fisheries Commission, Grant 04-3-043-59, Washington, D.C.
- Scattergood, L. W. 1952. The northern shrimp fishery of Maine. *Commercial Fisheries Review* 14(1):1–16.
- Schick, D. F. 1991. Pandalid shrimp distribution relative to bottom type and availability to research and commercial trawls in the Gulf of Maine. International Council for the Exploration of the Sea, C. M. 1991/K:8, Copenhagen.
- Schick, D. F., and M. Brown. 1997. Selectivity of northern shrimp trawls. Maine Department of Marine Resources, Completion Report, Project 93-NER-035, West Boothbay Harbor.
- Shumway, S. E., H. C. Perkins, D. F. Schick, and A. P. Stickney. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Kroyer, 1838. NOAA Technical Report NMFS 30.
- Sinclair, A., D. Gascon, R. O'Boyle, D. Rivard, and S. Gavaris. 1990. Consistency of some northwest Atlantic groundfish assessments. North Atlantic Fisheries Organization, Scientific Council, Report Document 90/96, Dartmouth, Nova Scotia.
- Stickney, A. P. 1980. Changes in fecundity of northern shrimp, *Pandalus borealis*, in the Gulf of Maine, 1963–1979. Maine Department of Marine Resources, Reference Document 80/11, West Boothbay Harbor.
- Terceiro, M., and J. S. Idoine. 1990. A practical assessment of the performance of Shepherd's length composition analysis (SRLCA): application to Gulf of Maine northern shrimp *Pandalus borealis* survey data. *Fishery Bulletin* 88:761–773.
- Thompson, W. F., and F. H. Bell. 1934. Effect of changes in intensity upon total yield and yield per unit of gear. Report of the International Fisheries Commission 8:7–49.